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Predation cost of a sexual signal in the threespine stickleback

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Short title: Predation cost of a sexual signal

Abstract

Much evidence exists for sexually selected traits reflecting various components of mate quality, but the factors that limit signal expression and ensure honest signaling are less well known. Predation risk has been proposed to be one factor that could constrain the elaboration of visually conspicuous signals and ensure honesty, but little evidence exists because of limitations of earlier used methods. We investigated using a combination of field observations and experimental work if a conspicuous sexual signal of the threespine stickleback *Gasterosteus aculeatus*, the red nuptial coloration of the male, increases predation risk. We compared the proportion of colorful males in the gut of a predator in the wild, the perch *Perca fluviatilis*, to that in the population, and found proportionally more red-colored stickleback in the gut. This indicates that the predator selectively preys on colorful males under natural conditions. To differentiate between the effects of color and behavior on susceptibility to predation, we experimentally investigated the attack behavior of the predator towards breeding stickleback males differing in coloration. We found the predator to preferentially attack more colorful males, independent of their behavior. These results indicate that predation risk is a cost of the sexual signal that could limit expression and influence the honesty of the signal as an indicator of mate quality.

Key words: Coloration, courtship, ornament, predation risk, reliable signaling, sexual selection

Introduction

Sexually selected signals have repeatedly been found to indicate mate quality, but the costs that limit signal expression and ensure honest signaling are less well known and usually assumed rather than demonstrated (Andersson and Simmons 2006; Giery and Layman 2015; Jennions et al. 2001; Kotiaho 2001; Zuk and Kolluru 1998). A commonly expected cost of visually conspicuous sexually selected signals is increased risk of predation. Bright colors, in particular, could attract the attention of predators and increase predation risk (Endler 1980). Yet, while some studies find sexually selected colors to increase the risk of predation (Giery and Layman 2015; Godin and McDonough 2003; Husak et al. 2006; Marshall et al. 2015; Stuart-Fox et al. 2003), others find not (Baird 2009; Gotmark 1993; Olsson 1993), and the importance of predation risk in limiting sexual color expression has remained equivocal.

One reason for the mixed evidence for a predation cost of conspicuous sexually selected colors could be limitations of the methods used. Most earlier studies have either been performed in the laboratory (Godin and McDonough 2003), or used static models presented to predators in the field (Gotmark 1993; Husak et al. 2006; Marshall et al. 2015; Olsson 1993; Stuart-Fox et al. 2003), which may not provide realistic estimates of predation risk. Laboratory conditions remove factors that could influence predation risk, such as obstructing vegetation or differences in the temporal or spatial distribution of predators and prey, while the use of static models removes the effect of behavior that can exacerbate or cancel out the effect of conspicuous colors on predation risk. A more fruitful approach would be to first determine the correlation between signal expression and predation risk under natural conditions, using wild organisms, to get an estimate of the possible magnitude of the cost, and then through lab or field experiments investigate the contribution of coloration to the predation cost by controlling for the effects of other factors, such as behavior. This could give a more realistic estimate of the predation cost of colors and indicate whether predation risk could limit expression and influence the honesty of color signals.

Here, we used a combination of field observations and experimental work to determine whether the conspicuous red nuptial coloration of the threespine stickleback male *Gasterosteus aculeatus* increases predation risk. Males develop a conspicuous carotenoid-based red nuptial coloration during reproductive activities: establishing territory, courting females to the nest, and caring for developing embryos and larvae in the nest (Wootton 1984). The red coloration is an honest, or reliable, indicator of various male qualities that are of interest to both mate choosing females and competing males, such as body condition and parasite resistance (Milinski and Bakker 1990), levels of antioxidant defenses (Pike et al. 2007), heritable immunocompetence (Barber et al. 2001), dominance and resource-holding potential (Candolin 1999a; Candolin and Tukiainen 2015), and parenting ability (Candolin 2000; Candolin et al. 2016). Yet, the costs that constrain the expression of the color, and prevent males from signaling dishonestly, are poorly known. Increased risk of predation has been proposed to be one factor, as males reduce their color expression when confronted with a predator (Candolin 1998). Moreover, males expose the red coloration to both gravid females and intruding males, which could expose the color also to unwanted observers. This could make the males more visible, or easier to single out, than more cryptically colored females or non-breeding males, which usually move around in shoals. However, whether predators detect, attack and catch colorful males more easily than dull males or shoaling stickleback, has remained unknown. Piscivorous fishes in shallow water, where stickleback breed, usually have color vision (Sabbah et al. 2013) and could selectively prey on colorful males.

We hypothesized that the red coloration of the stickleback male increases the risk of predation and that colorful stickleback males consequently are more often predated on by piscivorous fishes

than dull stickleback males or shoaling fish. To investigate if colorful stickleback in the wild are more often predated on than dull stickleback, we compared the proportion of red colored males in the gut of a common predator, the European perch *Perca fluviatilis*, to the proportion in the population. The perch has color vision, with high sensitivity to red, and is adapted to hunting in shallow waters (Cameron 1982). We carried out the study at a spawning site harboring both nesting and non-nesting, shoaling stickleback. To further examine if the predator preferentially attacks colorful stickleback males, independent of their behavior, we experimentally investigated the approach behavior of the perch towards two nesting stickleback males that differed in coloration and behavior.

Methods

The proportion of colorful males in the diet of perch

We caught perch during stickleback breeding season from a bay in the Northern Baltic Sea, Vindskär bay close to Tvärminne Zoological Station (60°N, 23°E). We used gillnets, 35 and 45 mm mesh size, to catch 28 perch larger than 20 cm (standard length) during 5 days at the end of May and beginning of June in 1997 (with 1-3 days between sampling, depending on weather). The perch is gape-limited and only larger perch prey on stickleback (Christensen 1996; Persson et al. 1996). The gillnets were set out in the morning at about 6 am, and fish were removed from the nets at 10 am and 2 pm, and at 6 pm when the nets were collected. The water depth at the sampling site was 2-3 m, and snorkeling had confirmed that perch were hanging out at this depth and making visits to more shallow water to catch stickleback. The perch were sacrificed immediately upon capture through decapitation and put in a cooler box on ice. They were brought to the lab, which is a 10 min boat drive away, where the gut content was inspected.

Stickleback in the gut that could be clearly identified as separate individuals, were larger than about 40 mm (smaller individuals are usually juveniles), and whose throat color could be determined without hesitation, were included in the analysis. This left us with 39 stickleback, from 25 perch, including both males and females (sex could not be determined for all stickleback). We could not reliably measure the area and brightness of the red coloration of all stickleback, because of different degrees of degradation of the fish, and, hence, only determined if the throat was red colored or not.

On the same day as the perch were caught, we sampled the stickleback population in the bay, using both Plexiglas traps (see description in Candolin and Voigt 2003) and a hand trawl, as fishing gear can differ in selectivity (Diana et al. 2006). We placed nine Plexiglas traps at depths of 30, 60 and 90 cm, three traps at each depth. The traps were set out immediately after the gill nets had been set out, and were collected at 5 pm before the gill nets were retrieved. The hand trawl was dragged in the bay at 8 am, avoiding locations with the traps. All caught stickleback were measured for body length (to the nearest mm) and inspected for the presence or absence of red nuptial coloration on the throat. We released all fish at the site of capture after measurements. Only adult stickleback (larger than 40 mm standard length) were included in the analysis. We caught 393 adult stickleback in the traps, and 354 with the hand trawl. We used a Chi-square test to compare the proportion of red colored stickleback in the gut of the predator to that in the population.

Predation risk experiment

To investigate whether the red nuptial coloration attracts perch, we recorded the approach behavior of a perch towards two nesting males that differed in red coloration. We caught stickleback at the start of the breeding season from the same bay as in the field investigation using Plexiglas traps. We transferred them within 30 min to holding tanks with flow-through of sea water, within an outdoor facility at Tvärminne Zoological Station with natural day light conditions. We fed the stickleback defrosted chironomid larvae once a day. Males with blues eyes, which indicates sexual maturity, were transferred to individual tanks (40 × 35 cm, water depth 30 cm) that contained a dish with sand and filamentous algae for nest building, and an artificial plant for hiding (see description in Candolin 1997). Twice a day, we presented the males with a gravid female, enclosed in a transparent, perforated plastic jar, for 15 min to stimulate nest building.

Perch larger than 25 cm were caught from the same bay using a hand-trawl and gill nets. They were transferred within 30 min using cooler boxes to flow-through holding tanks (150 × 60 cm, water depth 30 cm, 1-2 perch per tank) at Tvärminne Zoological Station. They were maintained for 1-3 days before used in the experiment. The perch were not fed during captivity to ensure they were hungry.

When stickleback males had completed nest building and developed red nuptial coloration, we selected two size-matched males (± 1 mm, n = 18 male pairs, mean size = 54.6 mm, SD = 2.6) that differed markedly in the red nuptial coloration: one bright male with a large area of bright red, and another dull male with only hints of red coloration around the mouth. Differences in coloration was ascertained by photographing the right lateral side of the males in a photographing box under standardized settings (Candolin 1999b; Heuschele et al. 2009). We dip-netted each male and placed him into a small glass box containing a black sponge that fixed him in position, and then placed the small box into a larger nonreflective dark box containing a camera with an inbuilt flash. The photographic procedure took <1 min. The similarity between human and stickleback vision allowed the use of the cameras trichromatic color system to analyze the red coloration (Rowe et al. 2006). From the digital photos, we measured the relative area of red (in relation to total area) using the software ImageJ 1.44 and the plug-in 'Threshold Color'. We used the HSB color model and selected red areas using the following values: hue = 0–21 and 238–255, saturation = 83–255, and brightness = 0–255, following the procedures outlined in Heuschele et al. (2012). The quality of the red color of the selected areas was calculated as R/(R + G + B) (Barber et al. 2000) using values from the plug-in 'Measure RGB' of ImageJ. Relative red area of bright males was 26.9% ± 1.7 (mean ± SE) and of dull males 2.6% ± 0.2, which differed significantly (mixed model with male pair as random factor: $F_{1,17} = 192.7$, $p < 0.001$). The quality of the red on bright males was 0.54 ± 0.01, and that on dull males 0.33 ± 0.01, which differed significantly ($F_{1,34} = 243.5$, $p < 0.001$).

We moved the selected males, together with their nesting dishes, to two tanks (70 × 40 cm, water depth 30 cm) in front of a larger tank (150 × 60 cm, water depth 30 cm), one male into each small tank (Figure 1). An opaque sheet prevented the transmission of visual cues between the compartments. The large tank was divided into two parts (150 x 30 cm) with a removable opaque sheet: in the back compartment we had placed a perch (25-28 cm standard length) the evening before, while the front compartment was left empty, except for 4 bunches of artificial vegetation present in both compartments (Figure 1). The stickleback could not see or smell the perch.

After the stickleback males had acclimatized to the experimental tanks for 1 h, we recorded their behavior for 15 min (in the absence of predator cues). We noted the time the two stickleback spent a) caring for their nests, including fanning and gluing the nest (nesting behavior), and b)

swimming outside the nesting dishes (general activity). After recordings, we lifted the removable divider in the large tank so that the perch could inspect both stickleback. We noted which male the perch first approached by orienting towards and then swimming towards, reaching within 5 cm of the divider to the male compartment. Immediately after the predator approach, we gently chased the perch back to the back compartment, using a long transparent rod, and lowered the removable opaque divider to enclose the perch in the back compartment (Figure 1).

After a 30 min break, we introduced a gravid female into each male tank, enclosed in a transparent, perforated plastic jar. We recorded, during 15 min, the courtship behavior of the males towards the females by noting a) number of zigzag bouts towards the female, b) number of leads to the nest, c) number of fanning bouts at the nest, d) time spent fanning, e) number of bites at the jar enclosing the female, and f) total courtship time (see Candolin 1997 for detailed description of the behaviours). After the 15 min, we lifted the removable divider in the large tank and allowed the perch to inspect the courting stickleback. We noted which male the perch first approached, within 5 cm of the divider. We calculated principal components for the six stickleback courtship behaviors as these were correlated (Table 2).

Each stickleback was used only once. Six perch were used in the experiment, and each perch was subjected to three trials with different male pairs, with the location of the two stickleback male categories (colorful or not) alternated between replicates. To test whether the predator approached the more colorful male more often than expected by chance, we used generalized linear mixed models (GLMM) with binomial error distribution and attacked (1) or not attacked (0) as response variable, male pair and predator identity as random factors to correct for dependencies within male pairs and predators, and coloration as a binary fixed factor (colorful or not). To test if the predator approached the more colorful male more often during courtship than before courtship, the two stages were inserted as a fixed factor into the GLMM. To test if male traits influenced which male the predator first attacked, the recorded behaviors were inserted as covariates and coloration as binary fixed factor in the GLMM.

Only healthy stickleback and perch, with no signs of diseases or injuries, were used in the experiment. All stickleback and perch were in good condition at the end of the experiment and released at the site of capture. This study was approved by the Animal Care Committee of the University of Helsinki (54-03), and conducted according to national guidelines.

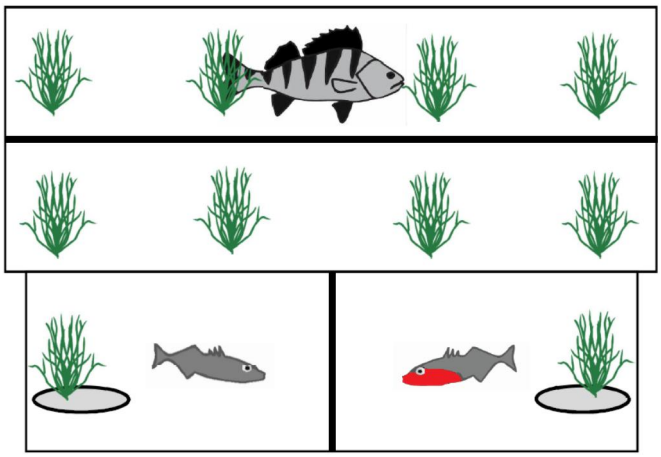

Figure 1. The experimental settings with two stickleback males with their nesting dishes, and the perch in the larger tank behind an opaque divider, which was removed during predator exposure. The two stickleback males were separated by an opaque sheet that prevented the transmission of both visual and olfactory cues. The fishes are not drawn to scale.

Results

Field investigation

We caught 28 perch (20-33 cm standard length, mean = 25.6 cm, SD = 3.6) that had remains of 39 adult stickleback in their gut whose color on the throat could be unambiguously determined. The proportion of red-colored stickleback was higher in the gut of the perch (28 out of 39 stickleback) than in the catches from the Plexiglas traps (96 out of 393 stickleback, Chi-square test $x2 = 38.90$, $p < 0.001$), or in the catches from the hand trawl (73 out of 354 stickleback, $x2 = 48.18$, $p < 0.001$, Figure 2a). The proportion of colorful stickleback did not differ between the catches from the traps and the hand trawl ($x2 = 1.54$, $p = 0.21$).

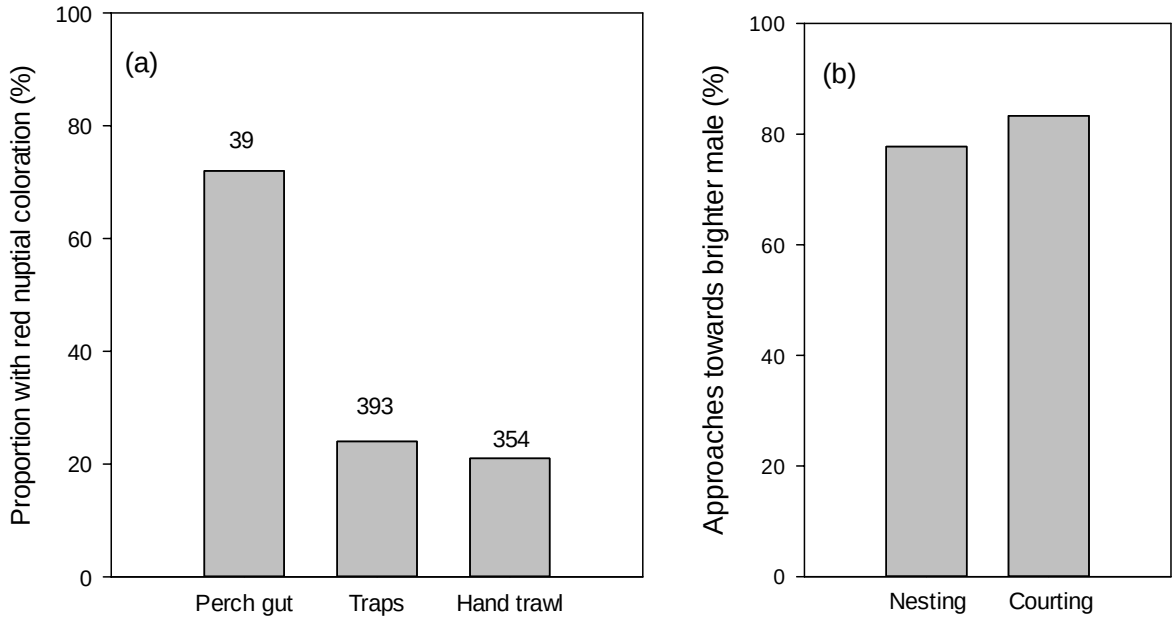

Figure 2 a) The percentage of adult stickleback with red-colored throats in the gut of perch and in the catches from the traps and the hand trawl. Numbers above bars give number of adult stickleback inspected. b) The percentage of times that the predator approached the brighter stickleback male rather than the dull male when the males were engaged in nesting activities and when courting a female. Dependencies with the six predators are not shown.

Predation risk experiment

The perch approached the brighter male more often than the dull male both before female presentation (GLMM: $F1,34 = 9.74$, $p = 0.004$) and during courtship ($F1,34 = 13.0$, $p = 0.001$, Figure 2b). The bright and the dull male did not differ significantly in nesting behavior before female presentation (GLMM: $p > 0.1$ for both recorded behaviors), but the brighter male had higher courtship activity than the dull male ($F1,17 = 8.90$, $p = 0.008$). However, courtship behavior did not alter perch behavior, as the perch approached the more colorful male both before female presentation (when the males were not courting) and during courtship (GLMM: $F1,34 = 0.19$, $p = 0.66$). Moreover, coloration was a stronger predictor of predator approach than the behaviors recorded, both before female presentation and during courtship (Table 1), with courtship activity

measured as the first principal component PC1 from a principal component analysis of the six courtship behaviors (Table 2). Courtship appeared to amplify the effect of coloration on predator approach behavior, as suggested by a close to significant interaction between coloration and courtship (Table 1).

Table 1. The dependence of perch approach behavior on male red nuptial coloration and behavior when a) nesting in the absence of a female, and b) courting a female. N = 18 male pairs.

a) Nesting				
Male trait	Coeff	SE	t	p
Coloration	2.42	0.83	2.93	0.006
Nesting behavior	<0.01	<0.01	1.07	0.292
Activity	<0.01	<0.01	0.35	0.725

b) Courting				
Male trait	Coeff	SE	t	p
Coloration	3.74	1.34	2.79	0.009
Courtship PC1	-0.97	1.03	-0.94	0.353
Color*Courtship	3.47	1.84	1.89	0.067

GLMM with binomial error distribution, with predator approaching vs not approaching as response variable, coloration as binary variable, and male pair and perch identity as random factors.

Table 2. Principal component analysis of the six courtship behaviours recorded. PC1 explained 64.6 % of the variation. PC2 explained 15.2 %.

Behaviours	PC1	PC2
Zigzags	0.762	-0.354
Leads	0.886	0.324
Fanning no.	0.874	0.294
Fanning time	0.925	0.300
Bites	-0.480	0.649
Time courting	0.813	-0.294

Discussion

The results show that the red nuptial coloration is associated with increased risk of predation. The proportion of red-colored stickleback in the diet of the perch was higher than the proportion in the population when sampled at a stickleback breeding site. This suggests that perch selectively preys on red-colored stickleback in areas where stickleback are gathering during the breeding season. The coloration could make stickleback more visible to the predator, or it could correlate with behaviors that increase conspicuousness or vulnerability to predators, such as courtship activity or lowered vigilance. Alternatively, the behavior of non-nesting, shoaling stickleback could lower their predation risk and cause the predator to prey more on nesting males, independent of their color. This would increase the proportion of red-colored males in the diet of the perch, as nesting males usually are nuptially colored.

The results from the predation risk experiment suggest that the red coloration of nesting males increases their predation risk independent of their behavior. The perch approached the brighter stickleback male more often than the dull one, and coloration was a stronger determinant of predator approach than behavior, both when the two males were caring for their nests and during courtship towards a female. Thus, the results from the field constitute a unique demonstration of a predation risk cost of a sexually selected coloration under natural conditions.

Courtship behavior showed a tendency to amplify the predation risk of the red coloration, as the perch tended to approach the brighter stickleback more often when the male also courted more actively. An amplifying effect of courtship on coloration has been documented in female mate choice, for both sticklebacks (McLennan and McPhail 1990) and other species (e.g. Candolin 2003; Hebets 2005; Reichert and Hobel 2015), but whether courtship amplifies the color also to unwanted observers - predators – has not been investigated. Previous studies on various taxa have found different reproductive traits to increase predation risk (Magnhagen 1991; Zuk and Kolluru 1998), but whether there are interactions among traits has not been considered. Yet, this is an important avenue of research, especially in changing environments where the impact of alterations in the efficacy or expression of some traits could then depend on other traits and possible changes in them. In particular, if multiplicative interactions occur, change in one traits could have a larger, or smaller, impact on reproductive success than given by its direct effect.

Another, not mutually exclusive explanation for the red coloration attracting the perch than visibility is that the carotenoid content of the red coloration indicates the nutritious value of the stickleback. This appears unlikely, however, as the coloration is highly flexible and males express it only when defending a territory. Males that have not yet established a territory, who adopt an alternative mating strategy, sneaking (Vlieger and Candolin 2009), or have a higher intake of carotenoids than needed for successful reproduction, can have a high carotenoid content but not express it (Candolin 1999b; Lindstrom et al. 2009; Pike et al. 2010). Moreover, females are larger than males (Wootton 1976) and should be preferred prey if perch were selecting prey with the highest caloric content. Thus, the most likely explanation is that the red coloration increases predation risk by catching the attention of the perch.

Whatever the cause of the preference of perch for colorful males, the results show that the red nuptial coloration incurs a fitness cost in terms of increased risk of predation. Together with an earlier study that found males to adjust their color expression to predation risk (Candolin 1998), the results suggest that the cost could limit the expression of the color and increase its value as a signal of predator avoidance ability (Zahavi 1975; Zuk and Kolluru 1998). The ability to avoid predation could in turn be correlated with other fitness related traits, such as metabolism and

foraging success (Krause et al. 1998; Metcalfe et al. 2016), immunocompetence and parasitism (Barber and Dingemanse 2010), and learning and cognitive abilities (Dall et al. 2005), and, hence, contribute to the maintenance of the color as a signal of the various fitness related traits documented in earlier studies (Barber et al. 2001; Candolin and Tukiainen 2015; Candolin et al. 2016; Milinski and Bakker 1990; Pike et al. 2007).

The results further suggests that changes in the predatory regime could alter the evolutionary trajectory of the color by altering the cost and benefit of expressing the color. This could explain differences in coloration among stickleback populations (McKinnon and Rundle 2002; Moodie 1972; Reimchen 1989), as proposed for other species with conspicuous colors, such as Bahamas mosquitofish, *Gambusia hubbsi* (Giery and Layman 2015; Heinen-Kay et al. 2015; Martin et al. 2014), and guppies, *Poecilia reticulata* (Endler 1980; Endler 1983). In the Baltic Sea, piscivorous fishes such as perch are declining (Bergstrom et al. 2016), which suggests that the cost of the red coloration could be decreasing. However, the consequence that a reduced cost will have for the population is unclear, as the benefit of the color is also decreasing, because of increased water turbidity and algae growth that reduces visibility (Candolin 2009; Candolin et al. 2016).

At a broader level, the results raise the intriguing question of what consequences the ongoing human-caused change of predatory regimes could have for the costs and benefits of sexually selected signals and, ultimately, for the process of sexual selection and the viability of populations. Considering the rate at which changes in predatory regimes are occurring (Dirzo et al. 2014), it is questionable whether evolutionary changes will be fast enough to adapt signals to the changes. Moreover, many other factors than predatory regimes are also changing, such as habitat structure and food quality and quantity (Scheffers et al. 2016; Walther 2010), which makes it challenging to predict the ultimate consequences of altered predatory regimes for populations.

To conclude, the results provide support for the common assumption that sexually selected signals increase predation risk in the wild. Thus, predation risk could be a factor that limits signal expression and ensures honest signaling in populations. At a broader level, the results suggest that changes in predatory regimes could alter signal expression and the process of sexual selection. Considering the rate at which humans are currently altering predatory regimes (Dirzo et al. 2014; Ripple et al. 2014), the consequences this could have for the viability of populations would deserve more attention.

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Data accessibility

Analyses reported in this article can be reproduced using the data provided by Johnson and Candolin (2017).

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